

**CYTOLOGICAL STUDIES OF THE BAR ALLELES OF
DROSOPHILA MELANOGASTER**

BY

RUSSELL PERRY HAGER

A. B., Bates College, 1934

M. A., University of Illinois, 1935

AN ABSTRACT OF A THESIS

**SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN
ZOOLOGY IN THE GRADUATE SCHOOL OF
THE UNIVERSITY OF ILLINOIS, 1941**

URBANA, ILLINOIS

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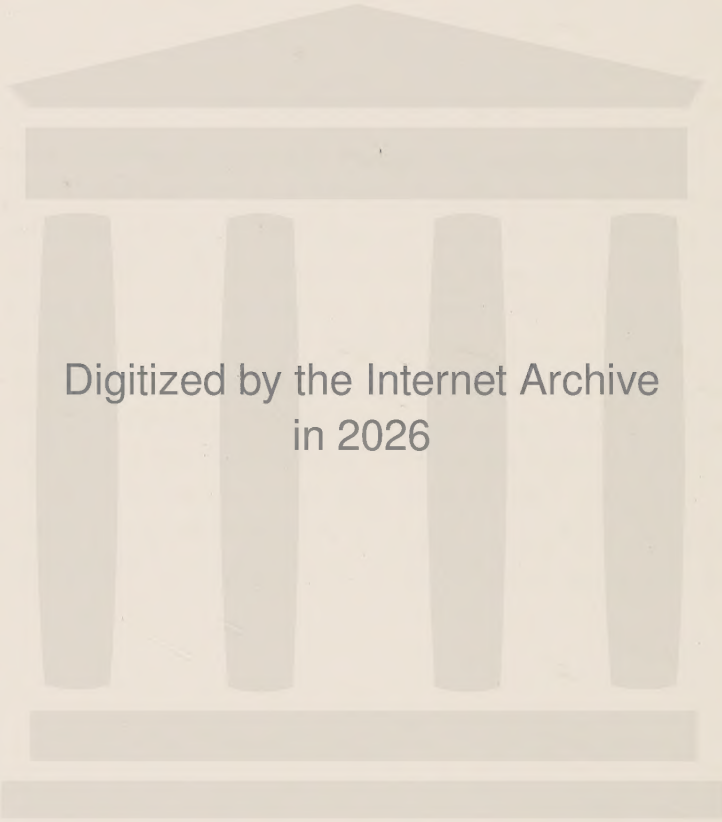
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I wish to express my sincere thanks to Professor Wilbur Marshall Luce, who suggested and directed this work, for his critical advice, assistance, and continued interest. I am also grateful to other members of the Department of Zoology of the University of Illinois, who have aided by their counsel; particularly to Professors Waldo Shumway and Clarence Erwin McClung for their kindness in reviewing critical cytological observations; and to Philip N. Bridges through whose kindness I was able to reexamine the original material used by his father, Calvin B. Bridges, as the basis for his description of the banding in the salivary gland chromosomes of double-bar.



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CYTOLOGICAL STUDIES OF THE BAR ALLELES OF *DROSOPHILA MELANOGASTER*

The series of multiple allelomorphs at locus 57.0 on the X-chromosome of *Drosophila melanogaster* includes the following major mutants: bar, ultrabar or double-bar, infrabar, double-infrabar, and bar-infrabar or infrabar-bar. The characteristic action of these mutants is a reduction in the number of units in the compound eye in comparison with the wild-type, round-eyed flies.

Sturtevant and Morgan, and later Sturtevant demonstrated that the mutations from bar to round and to double-bar are associated with crossing over between the recessive genes, forked and fused. Sturtevant showed the same relationship in the mutation from infrabar. In females heterozygous for both bar and infrabar, crossing over between forked and fused has been shown to be associated with the origin of a compound mutant, bar-infrabar or infrabar-bar depending on the order of the genetic factors.

As the result of the association of crossing over with the mutation at the bar locus, Sturtevant advanced the theory that the bar "gene" is single; the double-bar "gene", a duplication of bar; and the wild type, "no bar gene". Later investigators have considered bar to be the result of additional material inserted in the chromosome. Double-bar results when the inserted material is duplicated. Analysis of the banding in the X-chromosome of the salivary gland nucleus has been carried out by several workers. Muller and his co-workers demonstrated a duplication of the 16 A section in bar. Volotov described an insertion in the 16 A section in double-bar. Bridges described the duplication of the 16 A segment in bar and claimed to have identified a triplication of the 16 A segment in double-bar. He showed that the reverted-bar has only the single 16 A segment like the wild type.

The description of the salivary gland chromosomes led to the hypothesis that bar arose from round through unequal crossing over. In like manner bar was assumed to give rise to reverted-bar with a single 16 A section and double-bar with three sections.

Since the mutants containing infrabar are similar in their mutational behavior to those containing bar, and since the structure of the salivary gland chromosomes of these mutants had not been completely studied, their investigation was suggested to determine the nature of these mutations at the bar locus.

EXPERIMENTAL WORK AND OBSERVATIONAL DATA

In order to obtain large chromosomes, the larvae were raised at low temperatures on culture media enriched with yeast. Smears were prepared by the aceto-carmin method and mounted in diaphane. The banding in the various mutants and heterozygotes was carefully studied and analyzed.

Wild type or round. In all chromosomes containing the factor for round (+1119.1 and an attached-X stock carrying y) the bands were found to coincide with those mapped by previous workers.

Bar. In two stocks of bar, one a forked bar derived recently from bar-infrabar, the 16 A segment was found to be repeated.

Infrabar. The study of a stock of forked infrabar recently derived from forked bar-infrabar revealed a duplication of the 16 A segment apparently identical with that in bar.

Double-infrabar. Eight different stocks of double-infrabar were used in this study. Two had been derived recently from the forked infrabar stock used above. All had a reduced eye-size typical of the compound mutants. Only a linear duplication of the 16 A segment was identified. In this respect double-infrabar is similar to either bar or infrabar. There seems to be an increase in the width of the chromosome at the 16 A segment in comparison with that of bar, infrabar, or wild. The expected triplication could not be verified.

Bar-infrabar. The bar-infrabar stock used in this study mutates at a low frequency to both bar and infrabar. Its identity is therefore certain. Analysis revealed only a linear duplication of the 16 A segment. The bulge in that region appears to be swollen in comparison with wild, bar, or infrabar.

Double-bar. In a double-bar stock recently derived from the bar stock described above, only a linear duplication of the 16 A segment was observable. The swelling of the 16 A segment seems to be increased over that of bar, infrabar, or wild.

Reverted-infrabar and reverted-bar. In stocks of round-eyed flies obtained by reversion from infrabar and bar, only the single 16 A segment like that of the wild type was found.

Heterozygotes. In a study of all possible heterozygotes between wild, bar, infrabar, double-bar, double-infrabar, and bar-infrabar, the banding described above for the homozygotes was confirmed. In heterozygotes containing the wild type, the original 16 A segment is slightly stretched, and the two sections in the mutant member are compressed. It is difficult to distinguish the two homologs in the synapsed condition. Some chromosomes were found in which the synapsis was incomplete. In these the banding in each member could be easily identified and compared with that in the homolog.

DISCUSSION

As the result of the failure to find the triplication in the compound mutants, a scheme was devised to explain the relation between mutation and crossing over and the linear duplication with increased width. According to this theory the compound form is the result of partial non-disjunction of the X-chromosomes at the twin 16 A segments. The true double-bar, double-infrabar, or bar-infrabar would thus have four 16 A segments arranged two by two. In mutating simultaneously to round and a low bar or infrabar, a chromosome with one 16 A segment and a chromosome with three 16 A segments arranged two and one would result. The mutants with three segments should have lower facet counts than bar or infrabar as the case might be.

According to the prevailing theory of the nature of the mutants at the bar locus, it has been necessary to assume a position effect to explain discrepancies in the facet counts of genetic combinations which were assumed to be comparable.

On the basis of the theory just advanced the position effect assumption is unnecessary for there is a strict relation between the number and type of 16 A segment and the facet counts as determined by Sturtevant.

As the result of the evidence obtained in this study it seemed important to reexamine the original material used by Calvin B. Bridges as the basis for his description of a triplication in double-bar. Philip N. Bridges kindly sent me six of his father's ten slides of homozygous double-bar with one card containing the only notes made from the material. A very careful study of these has indicated that C. B. Bridges had misinterpreted the banding for there is evidence of only a duplication of the 16 A segment.

SUMMARY AND CONCLUSIONS

1. The banding in the X-chromosomes from the salivary glands of the following types of larvae has been described: round, bar, infrabar, double-infrabar, bar-infrabar, double-bar, and the heterozygotes between these.

2. The banding in the round type agrees with the previous descriptions.

3. The banding in bar and infrabar was found to be in agreement with expectation, a duplication of the 16 A segment.

4. The banding in the compound mutants, double-infrabar, double-bar, and bar-infrabar represents no more than a linear duplication of the 16 A segment. Bridges's original description was found to be in error.

5. The difference between the compound mutants and bar or infrabar has been described as an apparent increase in width of the 16 A bulge.

6. A theory is advanced that mutation from bar, infrabar, or the heterozygote between these to the compound forms is based on partial non-disjunction. In this manner, double-bar, double-infrabar, and bar-infrabar each have four of the segments per chromosome.

7. When Sturtevant's data on the facet counts in the various combinations is analysed on the basis of this theory there is no need to assume a position effect to explain the results.

VITA

Russell Perry Hager was born in Providence, Rhode Island, on October 17, 1912. He is the elder son of Ernest Russell Hager and Nellie Violet Perry Hager. His elementary school training was received in the City of Providence public school system and at the Henry Barnard School, connected with the Rhode Island State College of Education. His secondary school education was obtained at the Classical and Technical High Schools in the City of Providence.

At Bates College in Lewiston, Maine, he pursued a course of undergraduate study leading to the degree of Bachelor of Arts. In each year of his undergraduate training he received scholarship awards from the college. During his junior and senior years he was honorary assistant in biology.

Following his graduation from Bates College in June 1934, he was appointed assistant in zoology at the University of Illinois. During the academic year 1934-1935, he pursued a course of graduate study in zoology under the direction of the late Professor Charles Zeleny and received the degree of Master of Arts from the University of Illinois in June 1935.

He received an appointment as University Scholar from Brown University and continued his graduate study there during two academic years, 1935-1937, under the direction of Professors Herbert E. Walter and Paul B. Sawin. Throughout the academic year and summer of 1937-1938, he held an appointment as assistant in zoology at the University of New Hampshire and the Marine Zoological Laboratory of the University of New Hampshire at the Isles of Shoals. The following year he was appointed instructor at the University of New Hampshire. In that capacity he taught in the following courses: general zoology, general zoology for students of agriculture, anatomy and physiology for students of agriculture, histological technique, histology and embryology, and advanced

embryology. During the summer of 1939 he was an instructor at the Marine Zoological Laboratory of the University of New Hampshire at the Isles of Shoals. He conducted the course in histological technique.

In the fall of 1939 he returned to the University of Illinois as a University Fellow to resume graduate work under the direction of Professor Wilbur M. Luce. This work was continued through both semesters of 1939-1940, the summer of 1940, and the fall semester of 1940.

He has been elected to active membership in Sigma Xi and Phi Sigma.

